



Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles

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ABSTRACT

Areas of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks in the Black Hills can provide habitat for black-backed woodpeckers (*Picoides arcticus*), a U.S. Forest Service, Region 2 Sensitive Species. These outbreaks are managed through removal of trees infested with mountain pine beetles to control mountain pine beetle populations and salvage timber resources. To minimize impacts to black-backed woodpeckers while meeting management objectives, there is a need to identify characteristics of these areas that support black-backed woodpeckers. We examined the habitat associations of this species nesting in areas of beetle outbreaks in the Black Hills, South Dakota in 2004 and 2005. We used an information theoretic approach and discrete choice models to evaluate nest-site selection of 42 woodpecker nests at 3 spatial scales—territory, nest area, and nest tree. At the territory scale (250 m around nest), availability and distribution of food best explained black-backed woodpecker selection of beetle outbreaks versus the surrounding forest. Selection at the territory scale was positively associated with densities of trees currently infested by mountain pine beetles and indices of wood borer (Cerambycidae and Buprestidae) abundance, and was greatest at distances of 50–100 m from the nearest patch of infestation. At the nest-area scale (12.5 m radius around the nest), densities of snags positively influenced nest-area selection. Finally, at the nest-tree scale, aspen (*Populus tremuloides*) and 3–5-year-old ponderosa pine (*Pinus ponderosa*) snags were important resources. The association between abundant wood-boring insects and black-backed woodpeckers creates a difficult challenge for forest managers. In the absence of fire, areas of beetle outbreak might serve as the only substantial source of habitat in the Black Hills. Regulating insect populations via salvage logging will reduce key food resources to black-backed woodpeckers during nesting. Therefore, given the relatively infrequent occurrence of large-scale fire in the Black Hills, management should recognize the importance of beetle-killed forests to the long-term viability of the black-backed woodpecker population in the Black Hills.

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1. Introduction

Although, black-backed woodpeckers (*Picoides arcticus*) are widely distributed geographically (Bock and Bock, 1974) and use a variety of forest types, they are closely associated with standing dead forests containing an abundance of snags (see Dixon and Saab, 2000). In the western United States, black-backed woodpeckers appear to be nearly restricted to post-fire forests created by stand-replacing fires (Hutto, 1995; Raphael and White, 1984; Smucker et al., 2005). When considering the suppression of historical fire regimes throughout the range of black-backed

woodpeckers (Saab and Powell, 2005), this association with post-fire forest has prompted conservation concern by state and federal agencies. They are listed as locally rare and vulnerable to extinction and consequently are one of the Species of Greatest Concern in the Black Hills ecoregion (South Dakota Department of Game, Fish and Parks, 2006). Black-backed woodpeckers are also a “Sensitive Species” in Region 2 of the U.S. Forest Service and their habitat is given special consideration in the management of the Black Hills National Forest (USDA, 1996).

In addition to fire, areas of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, which are historically and currently a source of large scale disturbance in the Black Hills (Shinneman and Baker, 1997), also provide habitat for black-backed woodpeckers in the region (Bonnot et al., 2008). Black-backed woodpeckers have been reported nesting in beetle killed forests in other regions (e.g., the Pacific Northwest (Bull et al.,

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1986; Goggans et al., 1989) and Newfoundland (Setterington et al., 2000)). Forests with beetle outbreaks contain abundant snags that can provide food and nesting resources similar to recently burned forests. However, unlike recently burned forests, little is known about the specific resources within beetle-killed forests that support black-backed woodpeckers. For example, the role of food and nest-site availability in black-backed woodpecker nesting use of beetle killed forests remains unclear.

Forest managers have an interest in information that could help guide compromises between management of mountain pine beetle outbreaks and black-backed woodpecker conservation. Recent changes in management of the Black Hills National Forest place more emphasis on timber management for reducing fire and insect hazards (USDA, 2005). Current applications of salvage logging involve the removal of current and previously infested trees in an attempt to prevent insect dispersal and reduction in wood value. As with post-fire habitat, these activities could adversely affect conservation efforts for this Sensitive Species (Hutto and Gallo, 2006; Saab and Dudley, 1998; Saab et al., 2007). Thus, a better understanding of the important resources within outbreak areas is needed so managers can minimize impacts to black-backed woodpeckers when addressing threats to timber. For example, use of these areas by black-backed woodpeckers could be impacted if salvage logging reduced trees containing mountain pine beetle- or wood borer (Cerambycidae and Buprestidae) larvae, the primary foods of this species (Beal, 1911; Murphy and Lenhausen, 1998; Powell, 2000). Also, knowledge of the types of snags selected as nest sites or any characteristics of the forest around those nest sites could be considered when prescribing logging activities. Given the conservation status of black-backed woodpeckers and the need to manage threats to timber, it is critical that habitat associations of black-backed woodpeckers nesting in beetle killed forests be investigated to balance resource management.

With the objective of identifying resources important to black-backed woodpeckers in areas of mountain pine beetle outbreaks in the Black Hills, we evaluated nest-site selection by black-backed woodpeckers in these areas at three scales of selection. At a territory scale we compared resources within a 250 m radius around the nest to resources of similar scale from adjacent forests, allowing us to examine whether factors related to nest-site or food availability influence woodpecker use of beetle killed forests to other available forested areas. We evaluated selection of areas immediately surrounding the nest (nest-area scale) to help managers understand the importance of smaller scale features to nesting ecology of black-backed woodpeckers. Finally, we evaluated selection of the nest tree (nest-tree scale) to determine whether black-backed woodpeckers select a particular tree species, condition, or size of tree for nesting.

2. Materials and methods

2.1. Study site

The geographic scale of our study was the northern and central portions of the Black Hills National Forest in the Black Hills region of southwestern South Dakota (43°10' to 44°50' N and 103°20' to 104°50' W; Froiland, 1978). Elevation in the Black Hills ranges from 1066 m to 2207 m. The dominant forest type in the Black Hills is ponderosa pine (*Pinus ponderosa*), but stands of white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) also occur (Hoffman and Alexander, 1987).

Mountain pine beetles caused extensive ponderosa pine mortality throughout the Black Hills in the six years leading up to our study (Harris, 2004). By 2004, beetle populations were elevated across the entire Black Hills, with tree mortality in the northern and central portions occurring at epidemic levels from

coalescing areas of outbreak (Harris, 2004). Aerial surveys indicated that over 27 000 ha of forest were affected by outbreaks in 2004 (USFS, unpubl. data). Thirty-two percent of outbreaks occurred in patches greater than 100 ha in size. For comparison, during the three years from 2002 to 2004, the Black Hills had six fires that burned a total of 19 746 ha (USDA Forest Service, 2008).

We conducted our study in 2004 and 2005. For the 2004 field season, we identified 58 potential study sites using aerial surveys from a fixed-wing aircraft flown over the central and northern regions of the Black Hills in March 2004. We located areas of bark beetle infestation by the discoloration of foliage on dead ponderosa pines resulting from tree mortality two years prior. However, aerial surveys only provided the location of outbreaks in 2004, without information about their size or extent. For the 2005 field season we identified 54 study sites from remotely sensed imagery (USDA-Farm Service Agency, Aerial Photography Field Office, Salt Lake City, UT, USA) taken in the fall of the previous year. Sites identified for the 2005 field season averaged 195 ± 37 ha (SE).

2.2. Nest searches

We conducted area searches for black-backed woodpecker nests from 22 April to 1 July (the breeding season) in $\geq 90\%$ of the identified potential study sites of 2004 and 2005. Our methods were adapted from Saab and Dudley (1998) and we searched areas using crews of 2–4 members that walked transects spaced between 100 m and 200 m apart, which ensured we were within 100 m of all areas in the site. We used call playbacks at intervals of 100–200 m to locate birds. Call playbacks consisted of a recorded sequence of 3 black-backed woodpecker vocalizations: a series of chirps, a series of 3 drums, and a series of 3 rattles. We paused recordings for 10–20 s between separate vocalizations to listen for responses. Once observed, we used behavioral cues to follow individuals until we located a nest or determined they were not nesting. We recorded UTM coordinates for all nests using handheld GPS units with accuracy ≤ 10 m. We marked nests by flagging a nearby bearing tree at least 5 m from the nest tree and labeled it with the azimuth and height to the cavity.

2.3. Resource sampling

Following the nesting period, we used a matched case control design to estimate used and available resources for black-backed woodpeckers at 3 spatial scales—territory, nest area, and nest tree (Fig. 1).

2.3.1. Territory scale

At the territory scale, we compared resource attributes of used territories to available territories in the adjacent forest. We established available territories by selecting a tree, 750 m away in a random direction obtained using a random number generator (Fig. 1). Because, we were interested in black-backed woodpecker use of forest structure or characteristics, as related to nest-site availability and food availability, not physiographic or topographic differences (i.e., elevation, slope and aspect), we incorporated the concept of alternative availability, where criteria (e.g., physiographic and topographic variables) are used to limit choice sets to specific alternatives (Ben-Akiva and Bierlaire, 1999). Therefore, we only identified available territories with approximately the same elevation (within 30 m), aspect, and position on slope as the used territories to avoid differences in forest structure and composition resulting from these factors. Application of these criteria did not strongly limit our selection of available territories, rather this constraint was used to avoid extreme differences, such as comparing river bottoms to ridges, where forest structure would obviously be different. We assumed a 250 m radius (19.6 ha) was

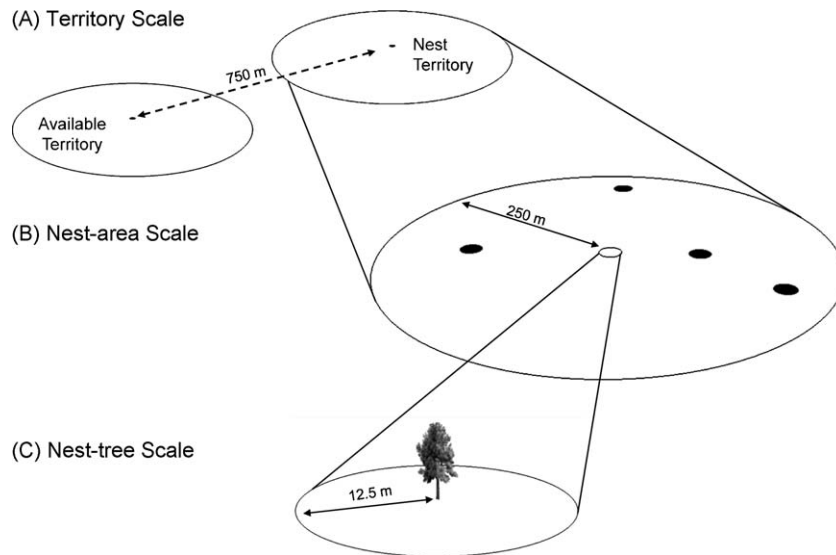


Fig. 1. Diagram of territory (A), nest-area (B), and nest-tree (C) scales of analysis of black-backed woodpecker nest-site selection in areas mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004–2005.

representative of the territory surrounding the nest or available tree (Fig. 1). Territory sizes are unknown for black-backed woodpeckers; therefore, we based our territory on estimates from the closely related American three-toed woodpecker (*Picoides dorsalis*), whose territory sizes in one study have been estimated at 11, 17, and 19 ha for 3 different pairs, respectively (Hogstad, 1977). Within each territory, we sampled 81 12.5 m fixed-radius plots (Mannel et al., 2006). We centered 1 plot at the nest or random tree and arranged the remaining plots at 50 m intervals along 16 transects, radiating out from the center at increments of 22.5°.

We recorded UTM coordinates and obtained various resource measurements within each plot. We tabulated numbers of all stems ≥ 2.54 cm diameter at breast height (dbh) and ≥ 1.4 m tall. For stems < 10 cm dbh, we recorded species and condition (live or dead). For trees ≥ 10 cm dbh, we recorded species, dbh (to the nearest 0.01 m), and condition. We used the classification described by Farris et al. (2002) to classify ponderosa pine snags according to the number of years since death (1 year, 2 years, 3 years, or ≥ 4 years).

To assess the importance of food resources in territories, we characterized the availability of the two main foods for black-backed woodpeckers, mountain pine beetles and wood borers (Dixon and Saab, 2000). Given indices can be useful measures of forest insect abundance (Knight, 1967), we recorded the density of trees containing active mountain pine beetle brood as an index of mountain beetle availability (Table 1). We estimated wood borer availability from egg niches, which are scars on trees where female wood borers have laid eggs (Furniss and Carolin, 1980). Adapted from Powell's (2002) method, we obtained an index of wood borer abundance by counting egg niches within a 30.5 cm wide strip, at a height of 1.7 m around the circumference of all pine snags ≤ 2 years old within the plot (Table 1).

2.3.2. Nest-area scale

We evaluated nest-area selection using a subset of the 12.5 m plots sampled at the territory scale to serve as used and available sites. According to a constrained design (Battin and Lawler, 2006), we compared resources from each nest (used) plot to a random subset of 4 available plots within the nest territory (Fig. 1). In addition to the data collected for the territory scale analysis, we incorporated the average percent of overstory canopy closure using a moosehorn (Garrison, 1949), from 49 points at each plot,

including 1 at plot center and 12 on each of the 4 cardinal axes at 1 m intervals.

2.3.3. Nest-tree scale

At the smallest scale we compared characteristics of the nest tree, including species, dbh, and condition, to other available trees within the 12.5 m nest plot (Fig. 1).

2.4. Spatial modeling of food resources

To determine whether the spatial distribution of food resources in the territories influenced selection, we characterized various measures related to size, number, and proximity of patches of food. We identified patches of mountain pine beetles and wood borers from plot level data by first using interpolation techniques to estimate their availability within 1 m cell size grids for each territory and then applying a threshold to those grids that distinguished areas of relatively high availability of food (i.e., patches). We used the completely regularized spline method in ArcGIS 9.0's Geostatistical Analyst (Environmental Systems Research Institute, Redlands, CA, USA) for interpolation, which uses the values from measured locations to predict values throughout the territory (Johnston et al., 2001). For each territory, we interpolated two grids. The first grid estimated the density of trees (per m^2) containing mountain pine beetles. Wood borer availability was estimated throughout each territory using the index of wood borer abundance from each plot. When delineating patches, we were unaware of any published measures of what abundances constitute patches of infestation by these insects. Therefore, we used a threshold value that was based on ArcGIS 9.0's natural breaks classification scheme (Environmental Systems Research Institute), where the value that delineated areas of high mountain pine beetle and woodborer availability from background levels within each grid was averaged across all grids to obtain a single standardized value. That standardized value served as the threshold which we applied to all grids. We also required that patches of mountain pine beetles have at least 1 tree containing mountain pine beetles present and patches of wood borers have a wood borer abundance index ≥ 1 . Black-backed woodpecker use of food may not be exclusive to either mountain pine beetles or wood borers; therefore, we merged both types to create a third patch that considered "food" in general. For each patch type (mountain pine

Table 1

Descriptions for variables used in models related to three scales of nest-site selection by black-backed woodpeckers in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004–2005.

| Hypothesis | Variable | Description |
|------------------------|-------------------|--|
| Territory scale | | |
| Nest-site availability | T1 | Density (per ha) of 1-year-old pine snags (≥ 10 cm dbh) in territory |
| | T2 | Density (per ha) of 2-year-old pine snags (≥ 10 cm dbh) in territory |
| | T3 | Density (per ha) of 3-year-old pine snags (≥ 10 cm dbh) in territory |
| | T4 | Density (per ha) of pine snags (≥ 4 years old and ≥ 10 cm dbh) in territory |
| | ASP | Density (per ha) of aspen snags (≥ 10 cm dbh) in territory |
| | SNAG | Density (per ha) of all snags (≥ 10 cm dbh) in territory |
| Food availability | MPB | Density (per ha) of trees containing mountain pine beetles (≥ 10 cm dbh) in territory |
| | WB | Index of wood borer abundance in territory (from egg niche counts in a 31 cm wide strip of bark at a height of 1.7 m on all pine snags dead ≤ 2 years) |
| | SUM_MPB | Estimated total number of trees containing mountain pine beetles in territory |
| | SUM_WB | Estimated overall index of wood borer abundance for the territory |
| | INF ^a | Mean cell value for patches of food |
| | AREA ^a | Total area (ha) of patches of food |
| | NUM ^a | Number of patches of food |
| | SIZE ^a | Minimum size (ha) of patches of food |
| | DIS ^a | Distance (m) to nearest patch of food |
| Nest-area scale | | |
| Nest-site availability | p1 | Density (per ha) of 1 year-old pine snags ≥ 10 cm dbh in 12.5 m radius plot |
| | p2 | Density (per ha) of 2 year-old pine snags ≥ 10 cm dbh in 12.5 m radius plot |
| | p3 | Density (per ha) of 3 year-old pine snags ≥ 10 cm dbh in 12.5 m radius plot |
| | p4 | Density (per ha) of pine snags ≥ 4 years old and ≥ 10 cm dbh in 12.5 m radius plot |
| | asp | Density (per ha) of aspen snags ≥ 10 cm dbh in 12.5 m radius plot |
| | snag15 | Density (per ha) of all aspen and pine snags ≥ 15 cm dbh in 12.5 m radius plot |
| | dbh | Mean dbh (cm) of snags ≥ 10 cm dbh in 12.5 m radius plot |
| | tree | Density (per ha) of trees ≥ 10 cm dbh in 12.5 m radius plot |
| | live | Density (per ha) of live pine trees ≥ 10 cm dbh in 12.5 m radius plot |
| | stem | Density (per ha) of all stems (live and dead) ≥ 2.54 cm dbh and ≥ 1.37 m in 12.5 m radius plot |
| | occ | Mean percent of overstory canopy closure from 49 observations on the 4 cardinal axis of the 12.5 m radius plot |
| | | |
| Food availability | mpb | Density (per ha) of trees containing mountain pine beetles in 12.5 m radius plot |
| | wb | Index of wood borer abundance in 12.5 m radius plot (from egg niche counts in a 31 cm wide strip, at a height of 1.7 m on all pine snags dead 2 years or less, on a per hectare basis) |
| Nest-tree scale | | |
| | SPECIES | Species of tree (pine or aspen) |
| | COND | Condition of tree (live or dead) |
| | DBH | dbh of tree (to the nearest 0.01 m) |

^a Separate variable for each type of patch: mountain pine beetle, wood borer, and food (mountain pine beetles or wood borers).

beetle, wood borer, and food in general), we calculated covariates related to the distance from the nest to nearest patch, the number of patches, the minimum size of patch, the total area of patches, and the mean level of availability for patches occurring in the territory (Table 1).

2.5. Model development

We used an information theoretic approach (Burnham and Anderson, 2002) to develop and evaluate models representing various hypotheses related to black-backed woodpecker nest-site selection in areas of beetle outbreak at the 3 spatial scales. We developed 67 territory-selection models to determine the relative support for 2 hypotheses: food- and nest-site availability (Table 1). Models related to nest-site availability included snag densities by species and condition. We constructed food availability models to reflect our general hypothesis of increases in availability positively influencing selection. Specific variables included density of trees containing mountain pine beetles and indices of wood borer abundance (Table 1). Models addressing the distribution in patches of food within territories were stratified by patch type (mountain pine beetle, wood borer, or beetle) and contained combinations of variables that included the total area, number, and minimum size of patches. We also included distance to the nearest patch. We included a cubic form of distance given that black-backed woodpeckers might select nests at intermediate distances from

the nearest patch as a compromise on avoiding increased activity around nests from other birds using the food patches while not having to gather food for nestlings from farther distances. Influences of variables associated with patches may depend on the level of infestation in the patches; therefore, we also included those interactions in our models.

At the nest-area scale, the candidate set included 23 models that addressed food- and nest-site availability as well as predation avoidance. Similar to territory selection, mountain pine beetle or wood borer availability in the nest-area may influence selection (Table 1). We also considered effects related to nest-site availability, including snag densities by species and age class; and a separate variable created to capture those snags thought to be suitable in size for black-backed woodpecker nesting (≥ 15 cm dbh [based on the smallest diameter nest tree observed in the study]) (Table 1). We included covariates related to predator avoidance, the mean overstory canopy closure (visibility to avian predators) and live tree density within the nest area (Table 1). Also, overall stem density within the nest area may be associated with selection as higher stem densities may increase predator concealment (Li and Martin, 1991; Nilsson, 1989).

At the nest-tree scale, we developed 10 models containing effects of tree dbh, species, and condition (live or dead) (Table 1). Black-backed woodpeckers nest in smaller sized trees (Harris, 1982; Saab and Dudley, 1998), possibly due to the higher percentage of more easily excavated sapwood present in smaller

trees (Bull et al., 1986). However, nest-tree size must still be large enough to adequately provide cavity space, thermoregulation and protection. Therefore, we included a quadratic form of dbh, because suitability of trees for nesting may be higher at intermediate sizes and lower at extreme sizes. Cavity nesters often select trees containing heartrot (*Phellinus* sp.) because the wood is easier to excavate (Jackson and Jackson, 2004); and heartrot (*Phellinus igniarius*) is prevalent in live aspen (Hart and Hart, 2001). Thus, we included an interaction effect between species and condition to examine whether the suitability of a live tree for nesting is conditional on the species.

2.6. Statistical analysis

Given the paired used/available design, we fit discrete choice models (Cooper and Millspaugh, 1999, 2001) related to nest-site selection at all 3 scales. Before fitting models using the conditional logit option in SAS's PROC MDC (SAS Institute, 2004), we tested for multicollinearity among covariates in each model with a tolerance value ≤ 0.4 (Allison, 1999). If multicollinearity was present in a model we removed affected covariates until correlation dropped below the threshold. We compared and ranked nest-site selection models at each scale using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i) (Burnham and Anderson, 2002). We addressed model selection uncertainty by calculating model-averaged estimates of the coefficients and their unconditional standard errors for the supported models in the 90% confidence set of candidate models based on Akaike weights (Burnham and Anderson, 2002). We estimated the relative importance of covariates from averaged models by summing the Akaike weights across all models in the 90% confidence set where the covariate occurred (Burnham and Anderson, 2002). A larger importance value indicates stronger support for that covariate relative to the other variables in the set. We interpreted model averaged estimates using odds ratios and their 95% confidence intervals (Hosmer and Lemeshow, 2000). We estimated relative prediction probabilities by varying explanatory variables of interest while holding other variables in the models at their mean values.

Because traditional goodness of fit measures are not appropriate for matched case control designs (Hosmer and Lemeshow, 2000, p. 236), such as discrete choice analysis (Boyce et al., 2002; Train, 2003), we evaluated the predictive ability of our nest-site selection models using a modification to Boyce et al. (2002) k -fold cross-validation design. With discrete choice models, the probability of a site's selection is conditional on the available choice set (Cooper and Millspaugh, 1999, 2001); therefore, we divided the data into 5 random subsets, each comprising approximately 20% of the choice sets, maintaining the used and available sites for each choice set. We successively removed one subset (the testing set), and refit the model using the remaining training data. Validation was based on the testing set, where we fit selection probabilities to all sites in each nest's choice set. Predicted sites were identified as having the highest relative probability of those within the choice set. We assessed the model's performance at each scale by determining the percentage of used sites in the testing set that were correctly predicted.

When conducting multi-scaled studies, cross-scale correlation can complicate interpretation when habitat variables at two or more spatial scales are correlated with each other (Battin and Lawler, 2006). Therefore, we used Spearman's rank correlation coefficients for variables from the most supported models at each scale to identify potential cross-scale correlations (Battin and Lawler, 2006). The presence of cross-scale correlation could result in erroneous conclusions about habitat selection at a given spatial scale because that habitat pattern is associated with selection at another scale.

Table 2

Support for models in 90% confidence set (based on Akaike weights) explaining black-backed woodpecker nest-site selection for 42 nests at 3 scales in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004–2005. Models are ranked based on Akaike's information criteria (AIC_c), ΔAIC_c , and Akaike weights (w_i).

| Model | | K | AIC_c | ΔAIC_c | w_i |
|-----------------|---|-----|---------|----------------|-------|
| Territory scale | WB | 1 | 17.53 | 0 | 0.51 |
| | MPB + WB | 2 | 18.85 | 1.33 | 0.26 |
| | T2 | 1 | 20.82 | 3.30 | 0.10 |
| | DIS _{food} ^{3a} | 3 | 22.20 | 4.67 | 0.05 |
| Nest-area scale | p1 + p2 + p3 + p4 + asp | 5 | 100.52 | 0 | 0.65 |
| | snag15 + dbh | 2 | 101.14 | 0.61 | 0.13 |
| | snag15 | 1 | 101.17 | 0.65 | 0.13 |
| Nest-tree scale | SPECIES \times COND + DBH ^{2a} | 5 | 192.98 | 0 | 0.97 |

See Table 1 for variable descriptions.

^a Also includes main effects terms for interaction and polynomial variables.

3. Results

3.1. Territory scale

We used 42 black-backed woodpecker nests ($n = 12$ for 2004, $n = 30$ for 2005) to evaluate nest-site selection models at the three scales. Among candidate models at the territory scale, those pertaining to food availability received more support than nest-site availability (Table 2). Models related to patches of food received greater support than patches of mountain pine beetles or wood borers individually. The most supported model contained the wood borer abundance index ($w_i = 0.51$) (Table 2). Model uncertainty existed, with 3 other models falling into the 90% confidence set of candidate models. Contained in those models were effects of the density of trees containing mountain pine beetles, 2-year-old pine snag density, and a cubic effect of distance to nearest patch of food (Table 2). The territory scale model, derived from averaging variables contained in the 90% confidence set of candidate models had good predictive ability, correctly classifying 95% of the used territories. The index of wood borer abundance was the most important predictor of selection for areas of beetle outbreak at the territory scale (importance value = 0.84) (Table 3). The mean index of wood borer abundance was 4 times greater in used territories ($\bar{x} = 73.2$; SE = 10.76) than in available territories ($\bar{x} = 17.2$; SE = 4.33). Densities of trees containing mountain pine beetles were also positively associated with territory selection as territories contained higher densities ($\bar{x} = 26.7$ trees per ha; SE = 4.38) than available ($\bar{x} = 8.6$ trees per ha; SE = 2.96). The presence of the distance term demonstrates how territory selection was greater for sites at intermediate distances to the nearest patch of food (Fig. 2).

3.2. Nest-area scale

At the nest-area scale, used areas averaged a lower mean dbh ($\bar{x} = 22.3$ cm; SE = 1.0) and contained higher densities of snags ≥ 15 cm dbh ($\bar{x} = 267.8$ snags per ha; SE = 30.96) than available areas. Three of the nest-area models received greater than 90% of the support of the candidate models (Table 2). The most supported model included effects of densities of pine snags in the 4 age classes and aspen snags ($w_i = 0.65$) (Table 2). Models containing the density of all snags ≥ 15 cm dbh and the mean dbh of trees in the nest-area also received support. Validation results showed the nest-area model correctly predicted used areas 61% of the time. All effects had marginal influence on selection, with the exception that every additional 3-year-old pine snag or aspen snag per hectare increased the odds of selection by 1% and 2%, respectively (Table 3).

Table 3

Model-averaged parameter estimates and unconditional standard errors, odds ratios, 95% confidence intervals, and importance values explaining black-backed woodpecker nest-site selection at 3 scales.

| Parameter | Category | Estimate | SE | Odds ratio | Lower CI | Upper CI | Importance |
|-----------------|-----------------------------------|-----------|----------|------------|----------|----------|------------|
| Territory model | WB | 0.120 | 0.056 | 1.13 | 1.01 | 1.26 | 0.84 |
| | MPB | 0.019 | 0.030 | 1.02 | 0.96 | 1.08 | 0.29 |
| | T2 | 0.033 | 0.032 | 1.03 | 0.97 | 1.10 | 0.11 |
| | DIS _{food} ^a | 0.010 | 0.011 | | | | 0.05 |
| | DIS _{food} ^{2a} | −5.37E−06 | 2.21E−05 | | | | 0.05 |
| | DIS _{food} ^{3a} | −5.37E−07 | 6.32E−07 | | | | 0.05 |
| Nest-area model | p1 | 0.004 | 0.002 | 1.00 | 1.00 | 1.01 | 0.71 |
| | p2 | 0.004 | 0.002 | 1.00 | 1.00 | 1.01 | 0.71 |
| | p3 | 0.009 | 0.004 | 1.01 | 1.00 | 1.02 | 0.71 |
| | p4 | 0.003 | 0.001 | 1.00 | 1.00 | 1.01 | 0.71 |
| | asp | 0.015 | 0.008 | 1.02 | 1.00 | 1.03 | 0.71 |
| | snag15 | 0.002 | 0.002 | 1.00 | 1.00 | 1.01 | 0.29 |
| | dbh | −0.011 | 0.016 | 0.99 | 0.96 | 1.02 | 0.15 |
| | SPECIES ^b | ∞ | – | – | – | – | 1.00 |
| Nest-tree model | COND ^b | ∞ | – | – | – | – | 1.00 |
| | SPECIES × COND ^b | ∞ | – | – | – | – | 1.00 |
| | DBH | 0.230 | 0.073 | | | | 1.00 |
| | DBH ² | −0.013 | 0.005 | | | | 1.00 |

See Table 1 for variable descriptions.

^a Pertains to patches of food.

^b No maximum likelihood estimates exist due to quasi-complete separation.

3.3. Nest-tree scale

Of the 42 nests, 32 (76%) occurred in ponderosa pine and 10 (24%) occurred in aspen. Most nests (86%) occurred in aspen or pine snags ≥ 3 years old. Nest trees averaged 25.2 cm dbh (SE = 0.88). The nest-tree model containing an interaction between tree species and condition and a quadratic form of dbh received 97% of the support (Table 2). The interaction variable had quasi-complete separation, which occurs when some combination of explanatory variables (the interaction of species and condition, in this case) correctly explains a subset of the data (Allison, 2004). This result indicates that the interaction of tree species and condition have a strong association with selection. Although estimates are unavailable for the species and condition parameters, estimates for dbh remain valid (Allison, 2004) and suggest that nest-tree selection by black-backed woodpeckers increased with decreasing tree size (Fig. 3). We were unable to validate the nest-tree model as estimates for some of the parameters were lacking. Cross-scale correlation was present, as higher densities of aspen snags occurred in the nest area when aspen was selected as the nest tree ($\rho_s = 0.860$, $P < 0.001$).

4. Discussion

Studies of black-backed woodpecker nesting habitat note the importance of both food and nesting resources (e.g., Dixon and

Saab, 2000), but when identifying processes driving nest-site selection, it is important to distinguish between these. Although standing dead forests might provide suitable nesting resources, not all contain an abundance of wood-boring insects. However, few have considered this distinction (Caton, 1996). Our results, which are based on the largest two year sample of nests in beetle killed forests that we are aware of, suggested that black-backed woodpeckers use areas of mountain pine beetle outbreaks in the Black Hills for the food resources rather than availability of nest-sites. Three of the 4 models supported for territory selection explicitly related to food availability. Although the density of 2-year-old snags in the territory appeared in the confidence set of models, most black-backed woodpeckers nested in aspen or pine snags ≥ 3 years old. Given that pine snags 2 years old are the most likely to contain wood borers in the Black Hills, this variable probably had more to do with food than nest-site availability. Our conclusion supports others that have found reductions in snags densities postfire resulted in reduced densities of cavity nesters, despite providing adequate nest-site habitat (Hutto and Gallo, 2006). Our results also suggest that beyond providing a source of food, mountain pine beetles create habitat for another and perhaps more important food source, wood borers.

While at the territory scale selection was most strongly associated with food resources, nest-area selection within the territory was influenced by the availability of snags for nesting. The probability of a nest area being selected increased with increasing densities of snags and decreased as tree diameter in the area

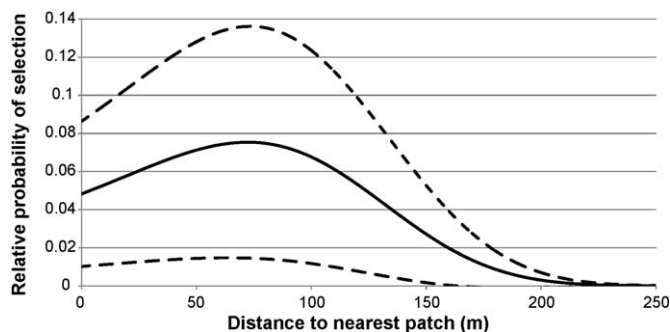


Fig. 2. Influence of distance to nearest patch of food on the relative probability of territory selection in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004–2005. Dashed lines represent bootstrapped 95% confidence intervals.

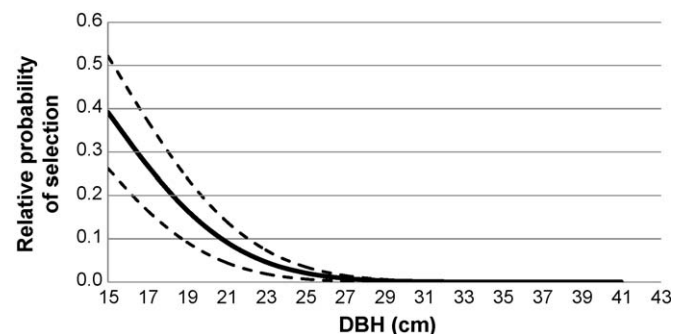


Fig. 3. Influence of tree diameter (dbh) on the relative probability of nest-tree selection in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004–2005. Dashed lines represent bootstrapped 95% confidence intervals.

increased. Similarly, Saab and Dudley (1998) found that black-backed woodpeckers in burned forests of Idaho selected areas with higher tree densities and smaller diameters than other cavity nesting species. Although effects were small, densities of aspen snags and to a lesser degree 3-year old snags had stronger effects than other snag classes. We observed 86% of the pairs nesting in either aspen or pine snags at least 3 years old, most of which showed evidence of heartrot, implying that this species selects nest areas containing many snags that may be easily excavated. Nearly as many nests occurred in the category of pine snags ≥ 4 years old suggesting this variable would have also been a strong predictor of selection. However, black-backed woodpeckers often select less decayed snags for nesting (Bull et al., 1986; Raphael and White, 1984; Saab and Dudley, 1998). Therefore, because the variable included much older, more decayed snags in addition to those 4 and 5 years old, it was probably precluded from showing a significant effect in the model. We suggest areas containing increased densities of aspen and moderately aged pine snags (3–5 years old) with minimal decay are important in nest-area selection by black-backed woodpecker.

Black-backed woodpeckers nested in live and dead aspen equally, whereas nests in pines occurred only in snags. Likewise, Mohren (2002) only found black-backed woodpeckers in ponderosa pine snags with heartrot. This disparity is most likely attributed to the presence or absence of heartrot as an underlying process for nest tree selection (indicated by the occurrence of quasi-complete separation), which supports our original motive for including the interaction. According to the model, the probability of a tree being selected as a nest tree decreased with size (Fig. 3). Mohren (2002) found black-backed woodpeckers in the Black Hills used trees of a similar size (25 cm dbh). However, the size of nest trees varies depending on region and tree species. For example, nest trees in ponderosa pine and Douglas fir (*Pseudotsuga menziesii*) averaged 39 cm dbh in Idaho (Dixon and Saab, 2000) and 37 cm dbh in ponderosa pine forests in Oregon ($n = 15$; Bull et al., 1986). Nests in a Wyoming study were mostly in lodgepole pine (*Pinus contorta*) and averaged 27 cm dbh (Hoffman, 1997). In the Sierra Nevada, nearly half of the nests occurred in Red fir (*Abies magnifica*) that averaged 45 cm dbh (Raphael and White, 1984).

In two instances a predictor of nest-site selection at one scale seemed to be an artifact of selection at another scale. In the first case, the seemingly counterintuitive selection of territories, such that nest sites are at intermediate distances (50–100 m) from patches of food, rather than closer to patches may be a result of this bird's selection for nest areas with high densities of suitable nest sites (Fig. 4). In the Black Hills, patches of infestation mainly consist of 1- and 2-year-old pine snags. If black-backed woodpeckers are choosing to nest in areas containing aspens or 3–5-year-old pine snags, then they would be forced to nest away from patches of infestation (Fig. 4). Second, the cross-scale correlation we observed suggests that the positive influence of aspen density at the nest-area scale may be a result of selecting aspens for nest trees. As Battin and Lawler (2006) describe, cross-scale correlation usually results from spatial autocorrelation of predictor variables. In this instance the clumped nature of aspen distribution in the Black Hills resulted in any nest in aspen being surrounded by high densities of aspens. Moreover, mountain pine beetle caused mortality creates forests with patchy distributions of different age snags, explaining why we observed that the category of snag used for nests was, in all cases, not only the most abundant in its respective nest plot, but was also more abundant in the nest plot than in the other available plots in the territory. Given habitat variables at any scale can affect selection at any other scale (Battin and Lawler, 2006), we suggest that the patterns of selection at the nest-area scale could be attributed to black-backed woodpecker selection of nest trees.

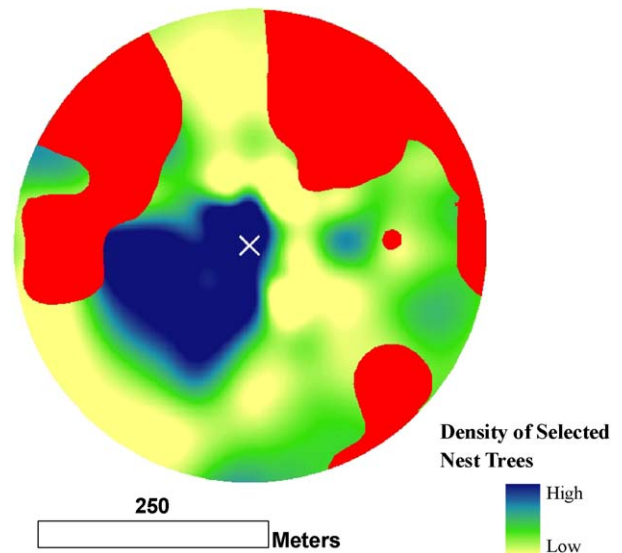


Fig. 4. Example of a black-backed woodpecker territory showing the common scenario of nests (represented by an "X") selected at intermediate distances from patches of mountain pine beetles or wood borers (red areas) and in areas containing increased densities of selected nest trees (aspens and pine snags ≥ 3 years old).

Therefore, conclusions about the types of trees important to nesting can be drawn from the nest-area scale, where aspens and 3–5-year-old pine snags were selected.

Identifying the relative importance of food availability versus nest-site availability for black-backed woodpeckers is probably most important when addressing the impacts of post-disturbance salvage logging on cavity-nesting communities (see Lindenmayer et al., 2004). Black-backed woodpeckers are consistently found at higher abundances in unlogged compared to salvage-logged standing dead forests (Hutto and Gallo, 2006; Morissette et al., 2002; Raphael and White, 1984; Saab and Dudley, 1998; Saab et al., 2007). These results are explained by the strong dependence on abundant snags for nesting and foraging (Hutto, 2006). Current snag management guidelines for forests were developed by considering only nesting requirements (Hutto, 2006; Thomas, 1979). However, recent research demonstrating lower woodpecker abundance in salvage-logged plots despite more potential nest snags per hectare than are necessary to maximize densities of primary cavity-nesters, led Hutto and Gallo (2006) to suggest that reduced food was more important than nest-site availability in these salvage-logged areas. Our results showing selection for food resources rather than nest-site availability supports Hutto and Gallo's hypothesis. In light of this recent evidence, snag retention guidelines for salvage logging may need to be revisited, as the number of snags required to meet food resource needs appears to be much greater than the number needed to meet nesting requirements for black-backed woodpeckers (Hutto and Gallo, 2006).

Based on our finding that food abundance is the most important factor in black-backed woodpecker territory selection, the overriding feature of site selection is a high abundance of food, primarily wood-boring insects (Scolytidae, Buprestidae, and Cerambycidae). Such a strong association with prey abundance explains how these birds reportedly use a variety of forest types over a wide geographic range, yet still be so restricted in their selection of specific habitats. Powell (2000) suggested that selection of foraging habitat by black-backed woodpeckers was best explained in terms of their diet breadth than associations with habitat types and we believe this relationship likely applies to all aspects of their resource selection. Our conclusion is further supported by other unique

observations of their natural history. Black-backed woodpeckers are considered one of the most arboreal woodpeckers (Burt, 1930), with distinctive adaptations for drilling for wood-boring insects (Burt, 1930; Spring, 1965). Also, despite the wide range of the species, black-backed woodpecker studies often note the concurrent presence of abundant wood-boring insects (Apfelbaum and Haney, 1981; Harris, 1982; Raphael et al., 1987). Selection for areas of abundant wood-boring insects explains the associations of black-backed woodpeckers with standing-dead forests, recently created by fire (Hutto, 1995; Saab et al., 2005; Smucker et al., 2005), bark beetle infestation (Bonnot et al., 2008; Bull et al., 1986; Goggans et al., 1989), and other disturbances (Short, 1974; Wickman, 1965). The importance of food also accounts for their ephemeral use of these areas, moving in only a short time after disturbance (Apfelbaum and Haney, 1981; Villard and Schieck, 1997), with occupation for only 3–5 years while bark beetles and wood borers are abundant (Harris, 1982; Murphy and Lenhausen, 1998; Saab et al., 2007).

The context and region of management is critically important in addressing black-backed woodpecker conservation at larger spatial and temporal scales. Because wood-boring insects may be an overriding factor in black-backed woodpecker ecology and insect species differ by region (Furniss and Carolin, 1980), incorporating geographic differences in insect abundance and availability and any environmental factors affecting them (e.g., frequency and timing of disturbance, forest type, or climate) is necessary. Such is the case in the Black Hills where the impacts of timber driven, mountain pine beetle management on the long-term viability of black-backed woodpecker populations is an important consideration. Outbreaks of mountain pine beetles and stand-replacing wildfire are natural components of the Black Hills ecosystem, but the highly suitable conditions they create are ephemeral; conditions that allow for abundant food last less than 5 years and will not be present again for decades. The occurrence of large scale fires is infrequent compared with natural disturbance regimes and beetle outbreaks might serve as the only substantial source of abundant wood-boring insects in the absence of fire. Therefore, because the need for controlling mountain pine beetle levels for the benefit of timber resources is clear, management that recognizes the relative importance of having beetle-killed forests in the Black Hills landscape when fire is absent might avoid impacts to the long-term viability of black-backed woodpecker populations. The relative role of areas of beetle outbreaks in sustaining black-backed woodpecker populations is likely dependent on (1) the availability of recently burned forests; (2) whether BBWO select beetle-kill areas when post-burn areas are available; (3) whether beetle killed areas are a “sink” habitat, information on which is still needed.

4.1. Management implications

The importance of food resources available to black-backed woodpecker nesting creates a challenge for forest managers that want to manage beetle outbreaks and avoid negative impacts to black-backed woodpeckers. Reduction of beetle populations in forests with mountain pine beetle outbreaks could negatively affect the suitability of those areas for nesting. Therefore, we advise against use of silvicultural treatments such as salvage logging in small outbreaks <20 ha, which is based on our territory scale analysis. For recently killed forests >20 ha we advise against silvicultural treatments during the black-backed woodpecker breeding season of May 15 through July 31 which would reduce direct impacts to food resources during nesting. When prescribing silvicultural treatments in outbreaks larger than 20 ha, we suggest managers retain areas containing suitable distributions of food and nest sites. Patches of mountain pine beetles or wood borers

interspersed at intermediate distances of 50–100 m with areas containing increased densities of aspens and 3–5-year-old pine snags should be considered for retention. Additionally, successful management of standing dead forests will require considerable improvement in our understanding of the interactions of salvage logging with wood-boring insects and wildlife that depend on them.

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